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Incorporating climate change into pest risk models for forest pathogens: a role for cold stress in an era of global warming?

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Abstract

Climate change may alter the distribution and activity of native and alien pathogens that infect trees and, in severe cases, cause tree death. In this study, potential future changes in climate suitability are investigated for three forest pathogens that occur in western North America: the native *Arceuthobium tsugense* subsp *tsugense,* hemlock dwarf mistletoe, and two alien invasive species, *Dothistroma septosporum*, the cause of red band needle blight or Dothistroma needle blight, and *Phytophthora ramorum*, the cause of sudden oak death or ramorum blight. Specifically, the software CLIMEX is used to calculate Cold-Stress, Heat-Stress, and Dry-Stress indices for each pathogen in 98,224 grid cells in North America. Downscaled climate projections from the general circulation models CGCM1, CSIROMk2, and HadCM3 drive forecasts for 2020, 2050 and 2080. These climate projections are then analyzed to forecast shifts in the geographic extent of abiotic stresses that are severe enough to directly kill pathogen propagules and prevent year-round establishment of these pathogens. Cold stress currently has a major impact on climate suitability for all three pathogens; heat stress is likely to become more significant in the future. I forecast that the geographic extent of cold stress will decline from its current levels by a constant 5% (± 1%) of all grid cells in each 30-yr projection horizon for all three pathogens. Forecasts suggest the extent of heat stress will increase concurrently by 4% (± 1%) in each 30-yr projection horizon. Drought stress shows no consistent trend over time. No disproportionate effect of climate change on the two alien invasive pathogens over the native is forecasted. These results suggest that forecasts of future climate suitability for pathogens based on historical climate normals are accurate for less than 30 yrs. Adaptive management strategies in forestry will be needed to respond as these changes unfold.

Keywords
Sudden oak death, red band needle blight, hemlock dwarf mistletoe, CLIMEX, alien invasive pathogens, exotic species

Introduction

Trees play pivotal roles in global carbon cycles. They remove significant amounts of carbon from the atmosphere annually and sequester fixed carbon for long periods (Bonan 2008; Chazdon 2008). Tree diseases can interfere with these processes. Disease, i.e., abnormal physiological function, in plants is the consequence of the interaction of a virulent pathogen with a susceptible host and a conducive environment. Forest health protection is a key strategy to adapt to climate change (e.g., Spittlehouse and Stewart 2003) and to ameliorate atmospheric carbon levels (Canadell and Raupach 2008; Nabuurs et al. 2007).

Climate change portends significant shifts in the structure and function of forests. In particular, ecological niche models for a number of tree species suggest future areas of climatic suitability will shift polewards in response to changes in temperature and moisture (Iverson et al. 2008; McKenney et al. 2011). For many species in general, dispersal capacity, demographic stochasticity, and cold-induced mortality are likely to dominate population processes at the leading, or expanding, edge of the range shift (Hampe and Petit 2005). At the rear, or contracting, edge, drought stress and genetic drift are likely to be among the dominant processes (Hampe and Petit 2005). Severe heat and drought events in western North America and elsewhere in the world already may have contributed to widespread tree mortality (Allen et al. 2010; van Mantgem et al. 2009).

Though climate change may be the ultimate cause of tree death, the proximate cause may be the activity of insects and diseases (Sturrock et al. 2011). Just as trees have specific temperature and moisture requirements, so do most pathogens. Qualitative assessments suggest that many forest diseases whose dynamics are directly governed by weather (e.g., Phytophthora root rot, Dothistroma needle blight, or Swiss needle cast) will become more severe if climate becomes warmer and wetter and less severe if conditions are warmer and drier (Kliejunas 2011; Sturrock et al. 2011). In contrast, diseases whose dynamics are mediated primarily by host condition (e.g., Armillaria root disease, Botryosphaeria canker, or pitch canker) will worsen if conditions become warmer and drier and will generally be unaffected if climate is warmer and wetter (Kliejunas 2011; Sturrock et al. 2011). Such qualitative assessments acknowledge substantial uncertainty as a result, in part, of a poor understanding of the epidemiology of many diseases, an inexact course of future climate change, and regional variation in the pattern and extent of climate changes (Boland et al. 2004; Dukes et al. 2009; Hepting 1963; Sturrock et al. 2011).

A general concern about the interaction of climate change and invasive alien species continues to grow (Driscoll et al. 2012; Dukes and Mooney 1999; Smith et al.

2012). Many invasive species are known to have broad environmental tolerances and high dispersal capacity. As a result, alien species effectively may be "pre-adapted" to future climate conditions and poised to dominate native species (Dukes and Mooney 1999). The potential significance of climate change for invasive alien pathogens of trees remains to be tested.

Pest risk maps illustrate how the likelihood and consequence of invasion by an alien species varies spatially within an area of concern (Venette et al. 2010). For many insects, weeds, and pathogens, this variation is likely to be driven, in part, by local and regional differences in temperature and precipitation. Some pest risk maps focus on an analysis of climatic suitability to characterize where an invasive alien species might become established if it were to arrive in an area, relying on the logical argument that there will be no impact if there is no establishment. If the forecast is driven by climatic normals, the resulting pest risk map will only be relevant in the future if temperature and moisture continue to fluctuate as they have for the previous 30 years. Pest risk maps would be substantially improved if they incorporated effects of climate change (Venette et al. 2010).

A number of analysts have incorporated climate change into forecasts of future climate suitability for invasive alien species (e.g. Baker et al. 2000; Desprez-Loustau et al. 2007; Watt et al. 2009). The common approach is to gather information about known geographic occurrences and absences of a species and to integrate these points with a database of current climactic norms. Climatological dimensions of the ecological niche are inferred from these data, and this inference is compared with downscaled output from general circulation models to determine if an area might be climatically suitable for an alien species in the future.

The purpose of this study was to compare the potential effects of future climate change on population stresses experienced by three forest pathogens: *Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp *tsugense*, western hemlock dwarf mistletoe, hereafter simply *A. tsugense*; *Dothistroma septosporum* (Dorog.) Morelet, the cause of Dothistroma (or red band) needle blight; and *Phytophthora ramorum* Werres, de Cock & Man in't Veld, the cause of sudden oak death and ramorum blight. *Phytophthora ramorum* is an oomycete that can infect more than 100 plant species and is new to Europe and western North America (Rizzo et al. 2005). The geographic origins of the pathogen remain unknown (Grunwald et al. 2012). As of 2013, the pathogen was established in North America in southwest Oregon (Curry Co.) and northwestern California (13 counties) and recovered from streams in Mississippi, Alabama, Florida, Georgia, and North Carolina. *Dothistroma septosporum* is a fungus with a cosmopolitan distribution and generally occurs wherever its hosts, several pine species (*Pinus* spp.), occur (Farr et al. 1995), though a particularly severe epidemic is occurring in British Columbia (Woods et al. 2005). The pathogen may be native to high elevations in Central America (Evans 1984) or the Himalayas (Evans 1984; Ivory 1994). *Arceuthobium tsugense* is a parasitic plant that is native to western North America, specifically western British Columbia, Washington state, Oregon, and northern California (Hawksworth and Wiens 1996). This mistletoe commonly infects western hemlock, *Tsuga heterophylla*

(Hawksworth and Wiens 1996). Under appropriate conditions, each of these pathogens can kill its host. I hypothesize that if native species tend to be more adapted to specific environmental conditions than alien invasive species, future climate-induced stresses should be more severe in North America for the native *A. tsugense* than on either alien species, *D. septosporum* or *P. ramorum*. I further hypothesize that different general circulation models should yield equivalent estimates of climate induced-stress. Abiotic stresses particularly those resulting from cold, heat, and drought, that act directly on these pathogens are the focus of this paper because these stresses are likely to dictate climatic bounds on the occurrence of these pathogens.

Materials and methods

Climate data. Climate normals and output from general circulation models downscaled to 10 arc-minutes were obtained from Worldclim.org, specifically mean monthly minimum temperature, maximum temperature, and precipitation. Downscaling had been performed using ANUSPLIN (Hijmans et al. 2005). At a resolution of 10 arc-minutes, each grid was approximately 18.6 × 18.6 km at the equator. I obtained climate data for four projection horizons – current, 2020, 2050, and 2080 – from three general circulation models – CGCM1, CSIROMk2, and HadCM3– under emission scenario b2a. This scenario assumes a low increase in greenhouse gas emissions with a corresponding increase in global average temperature of approximately 2°C by 2080. This change is less than changes suggested by other emission scenarios, but future climate is expected to change by at least this much. In total, data were procured for ten climate projections, i.e., three general circulation models x three projection horizons + current conditions. Current data primarily reflected the 30-yr climate normal from 1961–1990, though in some locations it may have reflected the period from 1950–2000 (Hijmans et al. 2005). There were 584,720 grid cells worldwide.

I restricted my analysis to North America, the only continent on which all three pathogens co-occur. Within the climate data sets, I functionally defined North America as those grid cells with centers occurring within the box with a northwest corner at 170°W and 80°N and a southeast corner at 50°W and 12°N. Individual grid cells were excluded from the analysis if projected minimum temperature was greater than the maximum temperature or if some climate data were missing. This standard ensured that exactly the same areas of North America were compared over time and left 98,224 grid cells for the continent. Data files were processed to be compatible with CLIMEX ver 2.0 (Hearne Scientific Software, South Yarra, Australia).

Estimation of abiotic stresses acting on pathogens. The "Compare Locations" feature of CLIMEX ver 2.0 was used to forecast physiological stresses experienced by *A. tsugense*, *D. septosporum*, and *P. ramorum* in response to extreme cold, heat, drought, and wetness now and in the future. CLIMEX calculated values for respective stress indices when temperatures or moistures exceeded species-specific thresholds. Stress also accumulated at species-specific rates. The final Cold-Stress, Heat-Stress, Dry-Stress, and

Wet-Stress indices potentially varied from 0 to 999. Values of 0 indicated no stress, and values of 100 indicated complete inoculum mortality from an abiotic agent. Values greater than 100 reflected severely stressful conditions (Sutherst et al. 2004). Grid cells with a stress index >99 were considered unsuitable for the year-round persistence of that pathogen. Sutherst and Maywald (1985) and Sutherst et al. (2004) provided specific formulas and details for the calculation of stress indices.

CLIMEX parameters for each species are reported in Table 1. CLIMEX parameters for *P. ramorum* were taken from Venette and Cohen (2006). Parameters for *A. tsugense* were developed through an iterative geographic fitting process initially described by Sutherst and Maywald (1985). The process began with a generic template for a temperate species. Geographic plots of CLIMEX indices were compared with the actual distribution reported by Hawksworth and Wiens (1996). I recursively modified CLIMEX parameters and compared with the known distribution until a qualitatively satisfactory fit was found.

CLIMEX parameters for *D. septosporum* were obtained from Watt et al. (2009) and modified slightly to reconcile with extant literature about the effect of heat on conidia viability. Gibson (1972) reported that conidia of what would now be recognized as *D. septosporum* could survive 9 wk at 30°C but only "several days" of dry heat at 35°C. I presumed that "several days" meant 6 days. Calculations based on these estimates indicated that heat stress would begin to accrue at 29.9°C, similar to the value from Watt et al. (2009), but the rate of stress accumulation would be 0.247 wk^{-1}. The modified parameter set qualitatively fit the distribution of *Dothistroma* reported by Watt et al. (2009).

Statistical analyses. All statistical analysis was performed in SAS 9.2 (SAS Institute, Cary, NC). Although individual grid cells are the observational units in this study, each observational unit is not independent in space. Thus, analyses focused on the propor-

Table 1. CLIMEX stress parameters for three forest pathogens.

Index	Parameter	*Arceuthobium tsugense*	*Dothistroma septosporum*	*Phytophthora ramorum*
Cold stress	TTCS=temperature threshold (°C)	-3.9	-30	-
	THCS=stress accumulation rate (wk^{-1})	-0.025	-0.05	-
	DTCS=degree-day threshold	-	-	15
	DHCS=stress accumulation rate (wk^{-1})	-	-	-0.0001
Heat stress	TTHS=temperature threshold (°C)	22	29.9	30
	THHS=stress accumulation rate (wk^{-1})	0.001	0.247	0.005
Dry stress	SMDS=moisture threshold†	0.3	0.10	0.2
	HDS=stress accumulation rate (wk^{-1})	-0.015	-0.005	-0.005
Wet stress	SMWS=moisture threshold†	2.5	-	2.5
	HWS=stress accumulation rate (wk^{-1})	0.002	-	0.002
Hot-wet stress	TTHW=temperature threshold (°C)	-	28°C	-
	MTHW=moisture threshold†	-	1	-
	PHW=stress accumulation rate (wk^{-1})	-	0.025	-

†, Moisture is expressed as a proportion of moisture holding capacity with values of 1 equal to saturation. Values > 1 reflect flooded conditions.

tions of grid cells in North America in which CLIMEX indices of cold stress, heat stress, wet stress or drought stress were >99. A grid cell that met one of these criteria was projected to be inhospitable for the year-round presence of the pathogen. The emphasis on grid cells with stress >99 ignores cases in which an abiotic agent might cause partial mortality of the population, but allows the analysis to focus on clear potential shifts in the geographic range in which a pathogen might be forecast to persist year-round. I refer to these proportions as the extent of stress. – Wet stress in North America was always 0 for each of the pathogens under the current and future climate, so wet stress was not analyzed statistically.

The extent of each stress from 2020 to 2080 was found to be normally distributed (Univariate procedure in SAS 9.2) and was analyzed first with repeated measures analysis of variance (Mixed procedure in SAS 9.2). General circulation model (n=3) and year (n=3) were included as main effects with a first-order auto regressive term to account for temporal covariance in the data. The experimental design did not allow for the testing of an interaction between year and general circulation model. Differences among forecasts for 2020, 2050, and 2080 were estimated using Tukey's multiple comparison test of least-squares means with $\alpha = 0.05$. Two-tailed t-tests for the difference between a population mean and a hypothesized population mean to compare results from 2020, 2050, and 2080, the population means, with results for the current climate, the hypothesized population mean, because no statistical sources of variation existed for stress estimates based on current climate. A Bonferroni-adjustment of α was applied to correct for multiple comparisons and ensure an overall $\alpha = 0.05$.

To compare changes in the extent of each stress over time among pathogens, I used mixed model analysis for linear regression (Mixed procedure in SAS 9.2). A first-order autoregressive error structure was used to account for autocorrelation in observations over time. Factors in the regression were general circulation model (n=4, now including current), pathogen (n=3), and time (n=4). Time was measured in 30-yr projection horizons, with 0 corresponding to 1990, 1 corresponding to 2020, and so on. All observations from the same levels of each general circulation model and pathogen effectively represent a single subject. The analysis assumes independence of observations from different subjects. Degrees of freedom were determined using the Kenward-Rogers approach. Paired contrasts were used to test for different intercepts and slopes among regression lines for each pathogen. A Bonferroni-adjustment of α was applied to correct for multiple comparisons and ensure an overall $\alpha = 0.05$.

All maps were created in ArcMap 9.3 (ESRI, Redlands, CA). For each stress index at each projection horizon, a grid cell is assigned the median stress value forecasted from the three general circulation models.

Results

Effects of climate change on stress projections for each pathogen. CLIMEX models driven by downscaled output from general circulation models suggest the geographic extent

of cold stress for *A. tsugense* will diminish in time (df = 2,4; F=24.52; P=0.006) while the extent of heat stress will increase (df = 2,4; F=103.22; P<0.001). The extent of drought stress is projected to be greater than it is currently, but no different from 2020 through 2080 (df = 2,4; F=1.13; P=0.408). Approximately 78.7% of grid cells are currently too cold for *A. tsugense* to persist (Fig. 1A). These cells generally fall north of 37°N latitude but not along the East or West Coasts (Fig. 2). The extent of cold stress will be reduced by 2020 (Fig. 1A), then generally occurring north of 39°N latitude , remain relatively unchanged through 2050 and again decline by 2080, when cold stress will generally occur north of 40°N latitude (Fig. 2). Heat stress currently affects 23.2% of grid cells (Fig. 1A), generally south of 42°N latitude (Fig. 2). This stress will increase to 30.6% in 2020 (Fig. 1A), generally south of 43°N latitude (Fig. 2), and continue to increase by an average of 3% of all grid cells in each subsequent 30-yr projection horizon through 2080 (Fig. 1A), by which time heat stress is projected to be severe throughout most of Mexico and the contiguous United States (Fig. 2). Drought stress for *A. tsugense* currently affects 47.9% of all grid cells in North America, generally west of 96° W longitude (Fig. 2). This extent will increase to approximately 50.3% by 2020 and remain at this level through 2080 (Fig. 1A).

For *D. septosporum*, the future extent of cold stress in North America will diminish through time (df = 2,4; F=59.12; P=0.001) while the future extent of heat stress will increase (df = 2,4; F=19.35; P=0.009); forecasts suggest the extent of drought stress for this pathogen will not change (df = 2,4; F=1.75; P=0.284). Currently, 19.3% of grid cells are inhospitable to *D. septosporum* because of cold, greater than in any future 30-year projection horizon for this pathogen (Fig. 1B). These cells generally occur north of 62°N latitude (Fig. 3). In each subsequent projection horizon, about 5.0% of all grid cells will lose cold stress, so by 2080, only 4.2% of grid cells will be too cold for *D. septosporum* to remain viable year-round (Fig. 1B). These cells are projected to occur in northern Canada and Alaska (Fig. 3). Heat stress currently affects 18.4% of grid cells, less than in any future projection horizon (Fig. 1B), grid cells with a Heat Stress index > 99 occur generally south

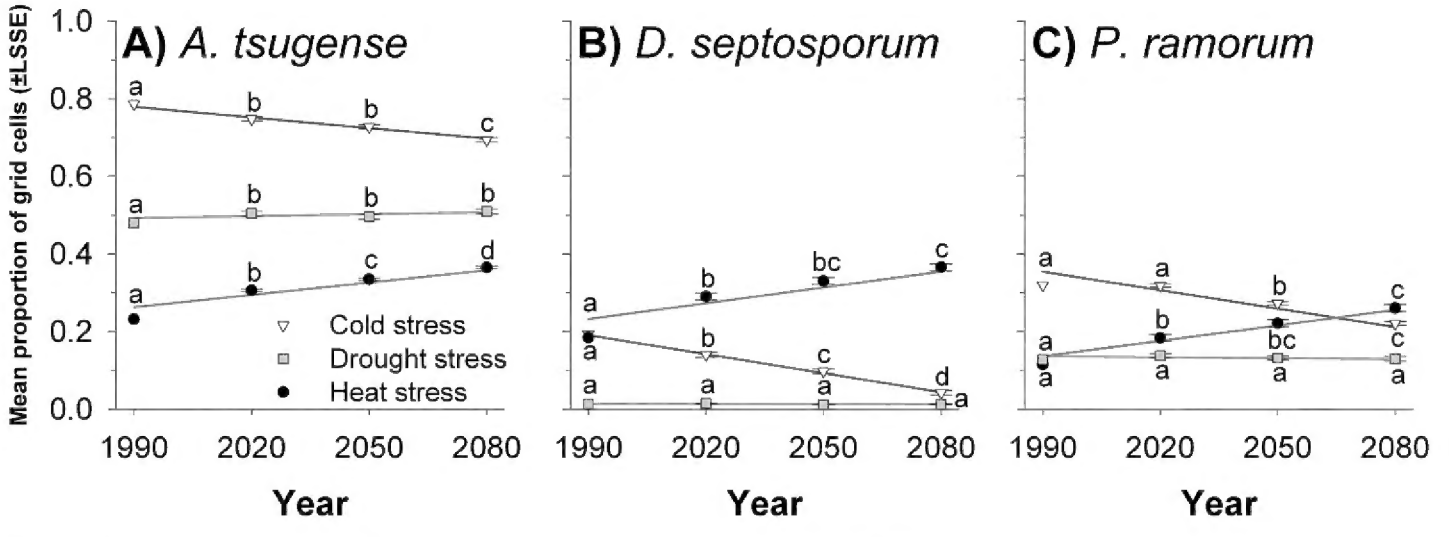

Figure 1. Proportion of North American grid cells with CLIMEX stress indices >99 over time for **A** *Arceuthobium tsugense* **B** *Dothistroma septosporum* and **C** *Phytophthora ramorum*. For each species, values for a stress with the same letter are not significantly different at $\alpha = 0.05$. Lines are predicted values from regression models described in Table 3. LSSE, least-squares standard error.

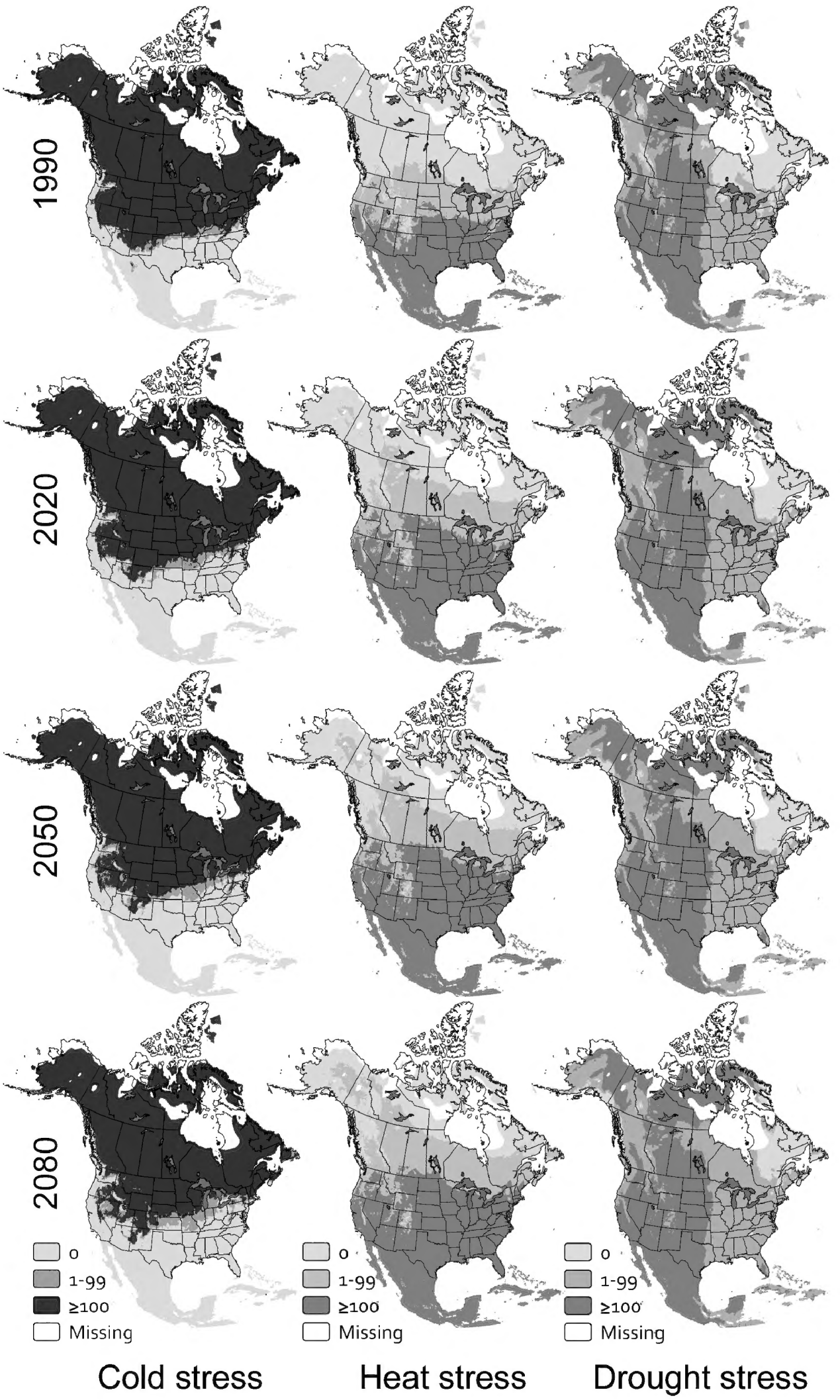

Figure 2. CLIMEX stress indices over time for *Arceuthobium tsugense* in North America.

of 37°N latitude (Fig. 3). The proportion of grid cells with heat stress will increase to 29.0% by 2020 and by an additional 3.8% of all grid cells in each subsequent projection horizon through 2080. By this time heat stress will extend throughout Mexico and the contiguous United States, except at high elevations and along the Pacific coast (Fig. 3). Drought stress is expected to affect approximately 1.3% of all grid cells now and through 2080, primarily in Baja California, Mexico and the desert Southwest, USA (Fig. 3).

For *P. ramorum*, the future geographic extent of cold stress will decline over time ($df = 2,4$; $F=93.57$; $P<0.001$) while the extent of heat stress will increase ($df = 2,4$; $F=19.04$; $P=0.009$). The extent of drought stress is not projected to change ($df = 2,4$; $F=0.54$; $P=0.619$). Currently, 31.9% of grid cells are too cold to maintain viable populations of *P. ramorum* year-round. These cells occur at high elevations and in northern portions of Canada and Alaska (Fig. 4). This extent of cold stress is forecasted to remain effectively unchanged through 2020. Then, the extent of cold stress will decline by 4-5% of grid cells in each subsequent 30-year projection horizon (Fig. 1C). By 2080, grid cells with a Cold Stress index > 99, will occur primarily in northern Labrador, northern Quebec, the Northwest Territories, the Yukon Territory, and northern Alaska (Fig. 4). Heat stress currently affects 11.5% of grid cells (Fig. 1C), generally south of 33°N latitude (Fig. 4). By 2020, the extent of heat stress is projected to increase to 18.4% of all grid cells and to continue to increase by approximately 4% of all grid cells in each subsequent projection horizon. By 2080, grid cells with a Heat Stress index > 99 will occur up to approximately 44°N latitude, except at high elevations (Fig. 4). Drought stress is expected to affect approximately 13% of all grid cells now and through 2080 (Fig. 1C), acting sporadically west of 99°W longitude (Fig. 4).

Effects of climate change on stress projections among pathogens. The three pathogens differed in the extent to which cold stress might currently constrain climate suitability for each species ($df = 1,12$; $F>34.38$; $P<0.001$ for three contrasts). The current extent of cold stress for *A. tsugense* is significantly greater than for *P. ramorum*, which itself has a greater extent of cold stress than *D. septosporum* (Table 3). The constant rate of change in the extent of cold stress over time was significantly less than 0 (Type 1 test of fixed effect of slope: $df = 3,6.83$; $F=22.90$; $P<0.001$), but did not differ among the three pathogens ($df = 1,6.83$; $F<2.90$; $P\geq0.134$ for three contrasts).

The extent to which heat stress might currently limit climate suitability for *A. tsugense* or *D. septosporum* was greater than for *P. ramorum* (Table 3; $df = 1,12.2$; $F>12.2$; $P\leq0.001$ for two contrasts), but the extent of heat stress that might currently act on *A. tsugense* was not different from that extent for *D. septosporum* ($df = 1,12.2$; $F=1.74$; $P=0.211$). The constant rate of change in the extent of heat stress over time was significantly greater than 0 (Type 1 test of fixed effect of slope: $df = 3,18.8$; $F=45.30$; $P<0.001$), but did not differ among the three pathogens (Table 3; $df = 1,18.8$; $F<1.32$; $P\geq0.265$ for three contrasts).

The three pathogens differed in the extent to which drought stress might currently limit climate suitability of each species ($df = 1,18.8$; $F>18.8$; $P<0.001$ for three contrasts). The extent of drought stress was greater for *A. tsugense* than *P. ramorum,* which in turn had a greater extent of drought stress than *D. septosporum*. The constant rate of

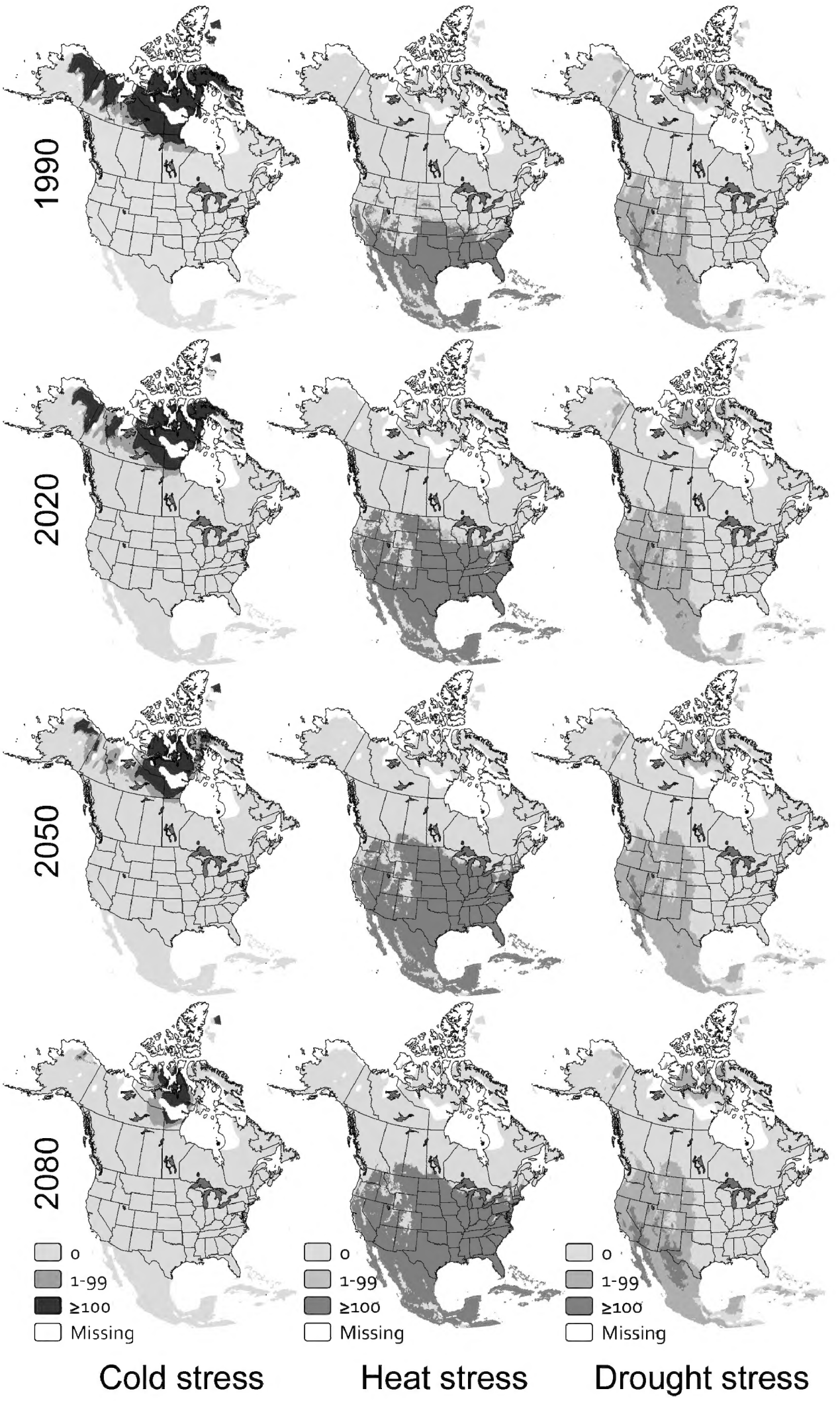

Figure 3. CLIMEX stress indices over time for *Dothistroma septosporum* in North America.

change in the extent of heat stress over time did not differ among the three pathogens (df = 1,23.8; F≤1.65; P≥0.361 for three contrasts) and was not different from 0 (Type 1 test of fixed effect of slope: df=3,23.8; F=0.61; P=0.614).

Effects of different general circulation models on stress projections for each pathogen. For *A. tsugense*, different general circulation models yielded different estimates of the future extent of cold stress (df = 2,4; F=13.57; P=0.016), heat stress (df = 2,4; F=12.52; P=0.019), and drought stress (df = 2,4; F=12.81; P=0.018). HadCM3 gave a greater extent of cold stress than CGCM1 or CSIROMK2; the extent of cold stress for *A. tsugense* forecasted from CGCM1 and CSIROMK2 were similar (Table 2). CGCM1 gave a lesser extent of heat stress than CSIROMk2 or HadCM3; the extent of heat stress from CSIROMk2 and HadCM3 were similar. Forecasts of the extent of drought stress based on CGCM1 were greater than HadCM3, but such forecasts based on CSIROMk2 were not different from either of the other general circulation models.

Different general circulation models yielded different estimates of the extent of cold stress for *D. septosporum* (df = 2,4; F=22.08; P=0.007) and *P. ramorum* (df = 2,4; F=93.57; P<0.001). For both pathogens, CSIROMk2 climate projections gave lower forecasts of the extent of cold stress than did CGCM1 or HadCM3 (Table 2). Though different general circulation models gave different estimates of the extent heat stress for *D. septosporum* (df = 2,4; F=9.30; P=0.031), they did not differ for *P. ramorum* (df = 2,4; F=5.83; P=0.065). For *D. septosporum*, the extent of heat stress based on CSIROMk2 was greater than the extent based on CGCM1; the projected extent of heat stress based on HadCM3 was not different from the other two general circulation models (Table 2). Estimates of the future extent of drought stress did not differ among general circulation models for *D. septosporum* (df = 2,4; F=4.47; P=0.102) or *P. ramorum* (df = 2,4; F=1.65; P=0.300).

Table 2. Effect of general circulation models on extent of forecasted abiotic stresses for three forest pathogens†.

Species	General circulation model	Cold stress (%±LSSE)‡		Heat stress (%±LSSE)		Drought stress (%±LSSE)	
Arceuthobium tsugense	CGCM1	71.6±0.6	A	32.3±0.3	A	52.5±0.6	A
	CSIROMk2	70.8±0.6	A	34.0±0.3	B	50.4±0.6	AB
	HadCM3	74.7±0.6	B	34.2±0.3	B	48.0±0.6	B
Dothistroma septosporum	CGCM1	9.7±0.6	A	30.0±0.9	A	1.1±0.1	A
	CSIROMk2	6.2±0.6	B	35.0±0.9	B	1.4±0.1	A
	HadCM3	12.1±0.6	A	33.6±0.9	AB	1.4±0.1	A
Phytophthora ramorum	CGCM1	29.6±0.5	A	20.0±0.9	A	14.1±0.6	A
	CSIROMk2	21.8±0.5	B	22.3±0.9	A	12.7±0.6	A
	HadCM3	29.8±0.5	A	24.2±0.9	A	13.1±0.6	A

†, Extent is measured as the percentage (elsewhere in this manuscript, proportion) of 98,224 grid cells in North America with a CLIMEX stress index > 99. Values represent the least-squares mean of three projection horizons: 2020; 2050; and 2080. Values for a species within a column followed by the same letter are not significantly different at α=0.05.

‡, least squares standard error.

Discussion

These models suggest that the geographic extent of heat stress will increase, cold stress will decrease, and drought stress will remain constant throughout North America for all three forest pathogens. Rates of change were measured by the slopes of regression lines relating the extent of stress to time. The fact that the rates of change were the same for each species was a surprise (Table 3). These species have different biological characteristics, which are reflected partially in the differences in CLIMEX parameters among species (Table 1). The different CLIMEX parameter estimates led to substantially different forecasts of the current extent of cold stress, heat stress, and drought stress among the pathogens (Table 3). The reason for the similarity in the rate of change among pathogens for each stress remains unknown and will become the focus of future investigations.

CLIMEX parameters for these three pathogens are generally consistent with the notion that alien species have broader climatic tolerances than native species. The differences between the temperature thresholds for the onset of cold stress (TTCS) and heat stress (TTHS) and between the moisture thresholds for the onset of dry stress (SMDS) and wet stress (SMWS) provide a measure of the breadth of temperature and moisture tolerances, respectively. In general, the native *A. tsugense* begins to experience heat stress when temperatures are cooler, cold stress when temperatures are warmer, and dry stress when soils are wetter than either alien species does. Different mechanisms of wet stress for *D. septosporum* and cold stress for *P. ramorum* complicate comparisons to the other two species.

With respect to my first hypothesis, I forecast that the native pathogen *A. tsugense* will experience more direct abiotic stress in the future than either of the alien pathogens (Fig. 1). This future difference, though, stems from the substantially greater extent of abiotic stresses currently experienced by *A. tsugense* than either alien pathogen

Table 3. Regression results for the proportion of North American grid cells with CLIMEX stress indices >99 over time†.

Stress	Species	Intercept (±LSSE)‡		Slope (±LSSE)	
Cold	*Arceuthobium tsugense*	0.78±0.02	A	-0.03±0.01	A
	Dothistroma septosporum	0.19±0.02	C	-0.05±0.01	A
	Phytophthora ramorum	0.35±0.02	B	-0.05±0.01	A
Heat	*Arceuthobium tsugense*	0.26±0.02	A	0.03±0.01	A
	Dothistroma septosporum	0.23±0.02	A	0.04±0.01	A
	Phytophthora ramorum	0.14±0.02	B	0.04±0.01	A
Drought	*Arceuthobium tsugense*	0.49±0.01	A	< -0.01±0.004	A
	Dothistroma septosporum	0.01±0.01	C	<0.01±0.004	A
	Phytophthora ramorum	0.14±0.01	B	< -0.01±0.004	A

†, Stress indices were calculated in CLIMEX, and values > 99 indicate locations where a species is projected not to persist year-round due to that abiotic stress. Values for a stress within a column followed by the same letter are not significantly different at $\alpha = 0.05$.

‡, least-squares standard error.

considered in this study. Future climate conditions do not disproportionately affect the rate of change in the extent of stress experienced by the native pathogen over the two alien species. Thus, I cannot conclude that climate change is creating greater areas of suitable climate for alien pathogens than for native pathogens.

My results suggest that cold stress currently is having a substantial effect on climatically suitable areas for *A. tsugense*, *D. septosporum*, and *P. ramorum* in North America. Cold stresses for *A. tsugense* and *P. ramorum* currently extend over a greater area than heat stress or drought stress (Fig. 1A, C), and for *D. septosporum*, the extent of cold stress and heat stress are effectively the same (Fig. 1B). Cold is likely to remain the most extensive abiotic stress for *A. tsugense* through 2080 (Fig. 1A) and for *P. ramorum* through approximately 2065 (Fig. 1C). For *D. septosporum*, however, cold stress will affect a smaller proportion of North America than heat stress by 2020. These results would support the value of additional research on the effects of cold temperatures on inoculum viability over time, especially for *A. tsugense* and *P. ramorum*.

With respect to the second hypothesis, I found that general circulation models differed in the extent of abiotic stress projected for each pathogen. These patterns were not always consistent among pathogens. For example, forecasts of cold stress from HadCM3 were significantly greater than from CGCM1 or CSIROMk2 for *A. tsugense*. For *D. septosporum* and *P. ramorum*, CSIROMk2-based forecasts suggested less cold stress than either of the other two general circulation models (Table 2). These results point to the value of considering multiple general circulation models when developing forecasts of where abiotic stresses might affect particular pathogens.

Climate change is likely to affect more than just the potential magnitude of abiotic stresses that act on these pathogens. Climate change may also directly affect the duration of temperature and moisture conditions that would be suitable or optimal for pathogen growth (Boland et al. 2004). Climate change may also indirectly affect the course of a plant-disease epidemic by altering the susceptibility of the host (Boland et al. 2004; Dukes et al. 2009; Hepting 1963; Sturrock et al. 2011). Trees under drought stress, for example, become more susceptible to infection by foliar pathogens than non-stressed trees (Jactel et al. 2012). Climate change may also alter the synchrony between inoculum production and the availability of sensitive plant tissues for infection (reviewed in Garrett et al. 2006). Nevertheless, the focus on direct abiotic stress that might act on forest diseases in the future is a reasonable first step. Such forecasts describe where pathogens are likely to occur year-round in the future and are useful, though imperfect, predictors of potential future impact (Boland et al. 2004).

Management decisions in agroforestry and perennial cropping systems span decades, and decisions made today rely on assumptions about future productivity and marketability of a crop. For example, the decision about which species or genetic lines to plant at a site is a management choice with ramifications potentially for the next 30 to 100 years (Pearse 1967). If trees are managed for carbon sequestration, rotations of 120 years might be optimal (Liski et al. 2001). In the past, managers might have

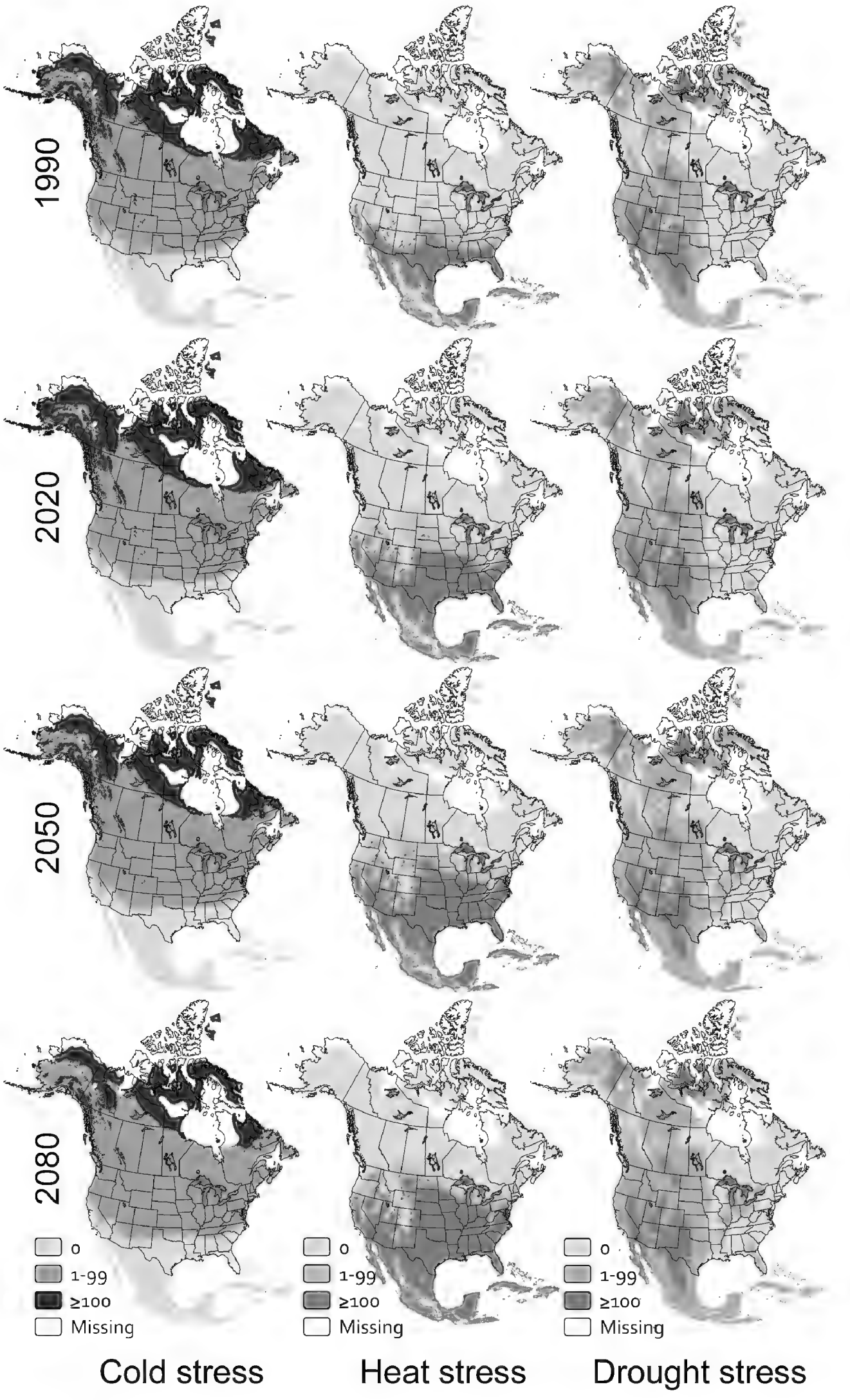

Figure 4. CLIMEX stress indices over time for *Phytophthora ramorum* in North America.

assumed that the environment would remain relatively stable over the lifetime of the crop. With this assumption, standard tree growth and mortality curves would yield suitably reliable forecasts of future harvests at different points in time (Dale et al. 1985). Minor losses of trees from pest and pathogen activity might be acceptable to some people, and outbreaks could be viewed as undesirable but not unforeseen events. Amidst growing evidence of a changing climate, managers are being encouraged to implement adaptive management strategies before the full effects of climate change manifest to improve the likelihood of meeting desired objectives (Spittlehouse and Stewart 2003). After tree planting has occurred, adaptive management options for forest health protection include removing diseased trees, thinning stands, applying pesticides, or shortening rotation length.

Pest risk maps that incorporate the effects of climate change should help land managers with longer-term planning activities and shorter-term management choices. For example, the maps developed as part of this project illustrate where abiotic stresses might exclude, or conversely might not exclude, three economically significant pathogens over time. So, these maps could be useful to decide whether trees with resistance to these pathogens should be planted, or if susceptible trees have already been planted, when to begin disease surveys. An additional benefit of these maps is that they capture complex dynamics (Figs 2–4). For example, while the total area that is at least marginal for *D. septosporum* is shrinking in North America, the area that is highly suitable is increasing (data not shown). So at a continental scale, climate change may be ameliorating some of the effects of this pathogen, but at a local or regional scale, climate change may be intensifying its effects. Qualitative characterizations of the effects of climate change are sensitive to the scales at which the assessments are made.

Forecasts of future disease activity based on climate normals will have limited utility over time. We found significant changes in abiotic stresses acting on each pathogen in each 30 yr projection horizon (Fig. 1). Our results suggest that models based on climate normals are likely to be useful for less than 30 yr.

CLIMEX focuses on abiotic drivers of population growth and death for ectothermic species. A benefit of this approach is that parameters have direct relevance to mechanisms underlying population change. Parameters estimated through inductive procedures, i.e., derived from known occurrences of a species, can suffer from some of the same limitations as other inductive species distribution models with respect to the vagaries of presence or absence records (Venette et al. 2010). But, unlike some other species distribution models, CLIMEX parameter estimates can be evaluated against extant literature on the autecology of the species or tested with appropriately designed experiments. A potential limitation of most species distribution models is that they fail to account for longer-term adaptation of a species to its environment, e.g. natural selection for drought or cold tolerance (Morey et al. 2013). More work is needed to account for additional sources of uncertainty in projections of the effects of climate change on the distribution and activity of forest pathogens and to express this uncertainty in ways that can be formally incorporated into decision-making processes.

Conclusions

Cold stress is likely to preclude the year-round establishment of *A. tsugense*, *D. septosporum*, and *P. ramorum* in many areas within North America.

With future climate change, the geographic extent of cold stress will diminish and allow for some northward movement in the range of climate suitability for these pathogens, but heat stress will increase and move southern range limits further north. Drought stress seems likely to act sporadically and not drive systematic changes the way temperature will.

The geographic extent of future cold stress, heat stress, and drought stress are forecasted to change at the same rate for the alien invasive pathogens *D. septosporum* and *P. ramorum* and the native pathogen *A. tsugense*. Future differences in the extent of abiotic stresses are the result of current differences.

The general circulation models CGCM1, CSIROMk2, and HadCM3 occasionally yielded different forecasts of the extent of stress for one of the three forest pathogens.

Forecasts of future pathogen occurrence or activity based on historical climate are meaningful for less than 30 yrs, less than the time horizon for many decisions in forestry.

Adaptive management strategies are needed for resource managers to remain responsive to realized future changes in the distribution and activity of forest pathogens. Pest risk maps that depict forecasts of these changes should provide useful guidance but are constrained by several sources of uncertainty.

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